# Comparison of $S_1$ with Open-Pollination Progenies in Selection for Yield in Crested Wheatgrass

John D. Berdahl* and Ian M. Ray

## ABSTRACT

Genetic gain from selection for high dry matter yield in most cross-pollinated forage grasses has been an elusive goal, in spite of sustained breeding efforts. This study was conducted to determine the value of one generation of self-pollinating ($S_1$) before selection for yield in crested wheatgrass (*Agropyron* spp.). Dry matter yields were compared at two locations near Mandan, ND, for synthetic populations derived from selection among and within $S_1$ or among and within open-pollination (OP) progenies from three source populations. Within each source population, the 20 parents used to produce $S_1$ progenies were in common with the 20 maternal parents of the OP progenies. Soil was a Parshall fine sandy loam (coarse-loamy, mixed, superactive, frigid Pachic Haplustolls) at Location 1 and a Wilton silt loam (fine-silty, mixed, superactive, frigid Pachic Haplustolls) at Location 2. In space-plant tests, $S_1$ family means for dry matter yield averaged 52% of OP family means, indicating high levels of inbreeding depression. In solid-seeded tests, yield differences between $S_1$– and OP-derived synthetic populations were significant ($P \leq 0.05$) for only one comparison. On the basis of three distinct source populations, we found that $S_1$ and OP families were both effective when used as the selection unit to choose high yielding parents for synthetic populations. Additional resources required to produce and evaluate $S_1$ families over OP families could not be justified in the crested wheatgrass source populations evaluated in this study.

INBREEDING HAS BEEN widely used in cross-pollinated species to help identify parents with superior genetic value. Kimberg and Bingham (1998) noted that increasing the level of homozygosity through inbreeding should facilitate both the elimination of deleterious recessive alleles and the selection for increased frequency of more favorable alleles in a population. Inbreeding studies with cross-pollinated forage grass species have had mixed results. Kalton et al. (1952) concluded that selection in inbred lines of orchardgrass (*Dactylis glomerata* L.) had doubtful value in orchardgrass improvement. McDonald et al. (1952) found that correlations for several traits in smooth bromegrass (*Bromus inermis* Leyss.) were consistently greater between $S_0$ parents and OP progenies than between $S_0$ parents and $S_1$ progenies. In meadow bromegrass (*Bromus riparius* Rhem.), de Araújo and Coulman (2002) found that OP and $S_1$ progenies were in closer agreement than either polycross and $S_1$ progenies or polycross and OP progenies for a wide range of traits. They concluded that the OP progeny test would be the most effective breeding procedure for selecting

parents for synthetic populations of meadow bromegrass. In timothy (*Phleum pratense* L.), Nielsen and Smith (1960) concluded that reselection of superior plants from large OP populations would likely be equally effective and more economical than would inbreeding and reselection during early stages of a breeding program. However, Murphy and Atwood (1953) selected $S_1$ progenies with excellent vigor and high levels of uniformity from a large population of smooth bromegrass. They concluded that elite $S_1$ parents should maintain superior performance in synthetics, where a low level of inbreeding would occur over several generations of seed increase. Thomas and Frakes (1967) compared clonal evaluation with five progeny testing methods in two populations of tall fescue (*Festuca arundinacea* Schreb.). They found that clonal evaluation, $S_1$, and single-cross progeny tests generally gave similar results, while OP, polycross, and $F_2$ ($S_1$ progeny of single-cross plants) progeny tests were generally the least useful in detecting differences among genotypes.

Genetic gain for high dry matter yield in most cross-pollinated forage grasses has been an elusive goal, despite long-term, multilocation breeding efforts. The objective of this study was to determine the value of one generation of self-pollinating before selection for yield in crested wheatgrass (*Agropyron* spp.). Yields were compared for synthetic populations derived from selection among and within $S_1$ and OP progenies that traced to common maternal parents in three populations of crested wheatgrass.

## MATERIALS AND METHODS

### Source Populations

Open-pollination and $S_1$ seed were harvested from 20 common maternal parents within each of three populations. An *A. desertorum* (Fisch. Ex Link) Schultes ($2n = 4x = 28$) source population with standard phenotype, ND-AD883, was a cycle-3 breeding population that originated from 47 accessions as described by Ray et al. (1994). Phenotype of a second *A. desertorum* source population, ND-AD862B, was intermediate between *A. desertorum* and *A. cristatum* (L.) Gartner. ND-AD862B was a cycle-2 breeding population that originated from the following 28 accessions: seven experimental strains from USDA-ARS, Lincoln, NE; five experimental strains from South Dakota State University, Brookings, SD; four experimental strains from Agriculture and Agri-Food Canada, Saskatoon, SK; and 12 plant introductions. An *A. cristatum* ($2n = 2x = 14$) source population with "Fairway" phenotype, ND-AC862, was a cycle-2 breeding population that originated from 79 accessions as described by Ray et al. (1997). The recurrent selection procedure employed before selection of maternal parents for this study was identical for all three populations. Accessions from each original population were randomly intermated in isolation nurseries in 1974 and then subjected to recurrent phenotypic selection for plant vigor,

J.D. Berdahl, USDA-ARS, Northern Great Plains Research Laboratory, P.O. Box 459, Mandan, ND 58554; I.M. Ray, Dep. of Agronomy and Horticulture, New Mexico State University, Las Cruces, NM 88003-0003. Received 5 May 2003. *Corresponding author (berdahlj@mandan.ars.usda.gov).

density of foliage cover, and seed yield under space-plant (0.9-m centers) conditions. Each cycle was generated by randomly intermating 300 to 400 selections from populations of approximately 2000 plants and then bulking an equal quantity of seed from each selected parent. Selection of 20 parents within each source population in 1991 was based on plant vigor and production of at least 20 $S_1$ seeds. $S_1$ seed was produced in the field by enclosing four to five inflorescences per plant in parchment bags. The bags were tied at the bottom, supported by stakes, and were shaken vigorously each day at approximately 1600 h during anthesis. Open-pollination seed was harvested from remaining spikes on the same maternal parents.

### Derivation of Synthetic Populations

Twenty $S_1$ and 20 OP families, each $S_1$ and OP pair tracing to a common maternal parent, were transplanted in 1992 on 0.9-m centers from each of the three source populations (ND-AD883, ND-AD862B, and ND-AC862). Each family was represented by four-plant plots, and families from each population were blocked together (sets in replicates) within each of three replicates. Plants were harvested individually in late June 1993, and green weights of surviving plants were averaged for each family. Derivation of synthetic populations is diagramed in Fig. 1. The five $S_1$ and OP families with the highest green weight yields averaged over replicates were selected from each of the three source populations. The highest yielding single genotype from each selected family in each of the three replicates was selected, resulting in a 15-parent synthetic (five selected families × single genotype from three replicates) from

$S_1$ family selection and a 15-parent synthetic from OP family selection within each population. Synthetics within each of the three populations were derived similarly from (i) $S_1$ families having the same maternal parents as the top five OP families and (ii) OP families having the same maternal parents as the top five $S_1$ families. Thus, a total of four synthetic populations were produced from each source population.

The 15 parents for each of the four synthetics from each source population were divided into five clonal ramets. Crossing blocks with five replicates in a randomized complete block design were established at isolated field sites for each synthetic in 1994. Seed was harvested from individual plants in 1995, 1996, and 1997, and equal quantities of Syn-1 seed from each entry were composited in 1997 for each synthetic.

### Performance of Synthetic Populations

Syn-1 seed of the 12 synthetics plus 'Nordan' (Hein, 1955), 'Hycrest' (Asay et al., 1985), and 'Parkway' (Alderson and Sharp, 1994) checks were used to establish performance tests at two locations near Mandan, ND, in 1998. Soil type at Location 1 was a Parshall fine sandy loam (coarse-loamy, mixed, superactive, frigid Pachic Haplustolls), and soil at Location 2 was a Wilton silt loam (fine-silty, mixed, superactive, frigid Pachic Haplustolls). Plots of each entry consisted of a single row 6.1 m long with a 60-cm spacing between plots. Seeding rate was approximately 100 pure-live seed per lineal meter of row. A randomized complete block design with 10 replicates was employed. Plots were harvested with a flail harvester in
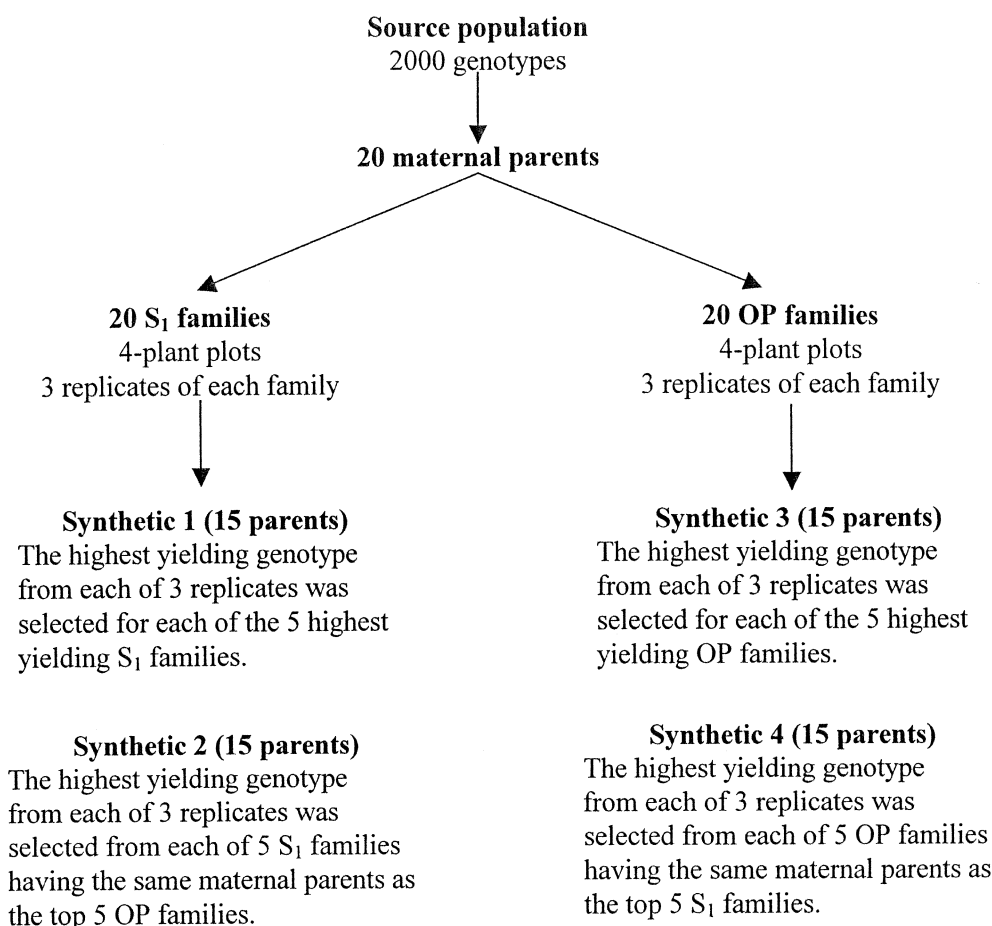


Fig. 1. Development of synthetic populations within a single source population.

**Table 1. Mean green weights of $S_1$ and OP families from 20 common maternal parents within each of three source populations of crested wheatgrass. Correlation coefficients are between means of 20 paired $S_1$ and OP families averaged over three replicates within each population.**

| Population | $S_1$ families | OP families | $r$ |
|---|---|---|---|
| | | g m$^{-2}$ | |
| *A. desertorum* (standard plant type) | 43 ± 15 | 102 ± 17 | 0.68** |
| *A. desertorum* (hybrid plant type) | 63 ± 18 | 126 ± 22 | 0.38 |
| *A. cristatum* | 70 ± 16 | 112 ± 18 | 0.53** |

** Significant at $P \leq 0.01$.

1999, 2000, and 2001 in late June, approximately 2 wk after anthesis, and dry-matter yields were recorded.

Individual plot values were analyzed in a split-plot in space (locations) and time (years) by a SAS PROC MIXED model (Littell et al., 1996) with entry and location considered to have fixed effects and years considered random. Differences among entries and locations plus the entry × location interaction were tested by appropriate F-ratios. Comparisons among appropriate paired $S_1$– and OP-derived synthetics were made using an independent $t$ test on individual plot yields from two locations and 3 yr ($n = 60$) (Steel and Torrie, 1980).

## RESULTS

### Performance of $S_1$ and OP Progenies

The initial evaluation of 20 $S_1$ and 20 OP families within each source population was conducted on plants that were space-planted on 0.9-m centers. Relatively high levels of inbreeding depression from one generation of self-pollinating were evident, with average yields of populations comprised of $S_1$ families ranging from 42 to 63% of those populations from OP families (Table 1). A large amount of variability was apparent within families, particularly some of the $S_1$ families. Correlation coefficients between $S_1$ and OP family means ranged from 0.38 to 0.68** for the three populations. Two of the five highest yielding $S_1$ and OP families had the same maternal parent in each of the *A. desertorum* source populations, while the five highest yielding $S_1$ and OP families in the *A. cristatum* population had no maternal parent in common.

### Performance of Synthetic Populations

Synthetics derived from $S_1$ and OP families in this study were representative of elite germplasm. Averaged

**Table 2. Tests of significance for fixed effects for dry matter yields of 12 crested wheatgrass synthetic populations tested over two locations and 3 yr.**

| Source of variation | Dry matter yield |
|---|---|
| Entry | ** |
| Location | * |
| Entry × location | ** |

\* Significant at the 0.05 probability level.
\** Significant at the 0.01 probability level.

over the three source populations and two locations, synthetics with parents consisting of $S_1$–derived genotypes had dry matter yields that averaged 92% of the mean of three commonly grown check cultivars. In comparison, dry matter yields of synthetics from OP-derived genotypes averaged 96% of the mean of the three check cultivars.

The entry and entry × location interaction effects were significant at $P \leq 0.01$, and the location effect was significant at $P \leq 0.05$ in the evaluation of dry matter yield of the synthetic populations that were generated from this study (Table 2). The largest shift in rank at the two locations was for the synthetic derived from selection within $S_1$ families that had the same maternal parents as the top five OP families in the *A. desertorum* population ND-AD862B. This synthetic ranked eighth in yield at Location 1 and 12th at Location 2 (data not presented). The entry X location interaction was not significant ($P \leq 0.05$) when the synthetic described above was not included in a SAS PROC MIXED analysis. The Spearman rank correlation coefficient for 3-yr mean yields of all entries at the two locations was 0.89**, and the Pearson correlation coefficient was 0.91**, indicating good agreement between locations.

Table 3 compares synthetic populations that have parents from $S_1$–derived genotypes with synthetics that have parents from OP-derived genotypes. In eight of nine comparisons, synthetics with OP-derived parents numerically outyielded synthetics with $S_1$–derived parents, although these differences were relatively small and significant ($P \leq 0.05$) in only one instance. This instance involved a comparison of selection among and within $S_1$ families with selection among and within OP families from the *A. cristatum* population (column 1 vs. column 2) (Table 3). Synthetics derived from selection within the five highest yielding $S_1$ families from each population were not significantly different ($P \leq 0.05$) in yield from synthetics derived from selection within

**Table 3. Dry matter yields of crested wheatgrass synthetic populations derived from $S_1$ and OP genotypes averaged over two locations and 3 yr.**

| Population† | Within $S_1$ families $S_1$ family selection | Within OP families OP family selection | Within OP families $S_1$ family selection | Within $S_1$ families OP family selection |
|---|---|---|---|---|
| | | kg ha$^{-1}$ | | |
| *A. desertorum* (standard plant type) | 3710 | 3766 | 3699 | 3652 |
| *A. desertorum* (hybrid plant type) | 3916 | 4141 | 4170 | 3652 |
| *A. cristatum* | 4610 | 4809* | 4737 | 4574 |

\* Significant difference ($P \leq 0.05$) between an $S_1$– and OP-derived synthetic population (column 1 vs. column 2) from the *A. cristatum* source population.
† Other comparisons:
Column 1 vs. column 3: Synthetic populations derived from selection within the five highest yielding $S_1$ families vs. selection within OP families having the same maternal parents as the top five $S_1$ families.
Column 2 vs. column 4: Synthetic populations derived from selection within the five highest yielding OP families vs. selection within $S_1$ families having the same maternal parents as the top five OP families.

OP families having the same maternal parents as the top five $S_1$ families (column 1 vs. column 3). Also, no significant differences ($P \leq 0.05$) were found between synthetics derived from selection within the five highest yielding OP families when compared to synthetics derived from selection within $S_1$ families having the same maternal parents as the top five OP families (column 2 vs. column 4).

## DISCUSSION

Evidence from this study confirms that both $S_1$ and OP families were effective when used as the selection unit to choose high yielding parents for synthetic populations in both diploid and tetraploid crested wheatgrass populations. One generation of self-pollinating should fix some deleterious recessive alleles, making it possible to eliminate plants that carry a high genetic load. Identification of other plants that carry an increased frequency of favorable alleles should also be enhanced. However, yield evaluation of $S_1$ families was difficult when working with the levels of inbreeding depression encountered in the crested wheatgrass populations that we studied. In space-planted tests, $S_1$ family means for dry matter yield were 52% of OP family means when the 20 $S_1$ and OP progenies in each population were averaged over the three populations (Table 1). Yields were variable and survival was low within many of the $S_1$ families. The coefficient of variability from an ANOVA of mean $S_1$ family yields (60 families, four plants each, 3 replicates) was 49% compared with 29% for OP family means. Low self-fertility in crested wheatgrass would make it extremely difficult to produce sufficient seed to provide an adequate evaluation of $S_1$ progenies. Murphy (1942) and Knowles (1950), based on relatively small numbers of $S_1$ progenies, also reported high levels of inbreeding depression for plant vigor and yield in both *A. desertorum* and *A. cristatum*. They concluded that self-pollinating as a breeding practice in crested wheatgrass held little promise in selection for combining ability of parents and yield of experimental strains.

Wilse (1951) pointed out that plant species that are normally outcrossing would be expected to maintain a high level of heterozygosity that would condition high levels of plant vigor. Our selection for high yield among $S_1$ families in crested wheatgrass suggested that we may have been selecting for heterozygous alleles that would help to maintain yield. In comparing yields of the top five $S_1$ families with OP families derived from the same maternal parents, $S_1$ families had green weights that averaged 69, 64, and 100%, respectively, of corresponding OP family yields for the *A. desertorum* population with standard phenotype, the *A. desertorum* population with

hybrid phenotype, and the *A. cristatum* population (data not presented). This reflects a considerable improvement in relative performance of selected $S_1$ families compared to the levels of inbreeding depression found for all 20 $S_1$ families within each population (Table 1). If increased levels of heterozygosity were realized through selection for high yield among $S_1$ families, this level of heterozygosity would not be maintained in corresponding synthetic populations after several generations of seed increase.

We conclude that use of $S_1$ families had no advantage over OP families in selection for dry matter yield in crested wheatgrass. Crested wheatgrass has low self-fertility and high levels of inbreeding depression, and additional resources required to produce and evaluate $S_1$ families over OP families could not be justified.

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